

SYSTEMATICS AND BIOGEOGRAPHY OF THE TYRANNID GENUS *TODIROSTRUM* AND RELATED GENERA (AVES)

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ABSTRACT. Of 32 Tody-tyrant species (family Tyrannidae), 14 comprise the genus *Todirostrum* and 12 are currently placed within *Idioptilon*. The remaining species represent six monotypic genera. *Todirostrum* species fall into two major species groups (labelled *cinereum* and *sylvia*), and the affinities of one additional, relict species (*capitale*) lie outside the genus. The distributional history of each species group can be approximately traced from the isolation of two ancestral populations. Alternating contraction and expansion of lowland South American forests, corresponding with dry and humid climatic phases, generated new species within each lineage. Their modern compositions and distribution patterns were determined by dispersal ability and competitive interactions between related species. Current distributions and plumage patterns appear to reflect the history of this radiation within *Todirostrum*.

Two relict species groups (one includes *T. capitale*, the other is an intermediate assemblage between *Todirostrum* and *Idioptilon* placed in the latter genus) illustrate the potential fate of many taxa in the rapidly radiating South American avifauna. As the number of species increases with cyclic production of new forms within lowland forest refuges, each faces increasing competitive pressure as it disperses. Certain species and whole lineages may be secondarily contracted into local distributions by dispersing, competitively superior relatives. The process culminates either in morphologic and ecological divergence by the inferior population, or in its eventual extinction. Intermediate stages in this "continental taxon cycle" are found in the Tyrannid group examined here.

Four specific taxonomic suggestions are offered in addition to comments on affinities within *Todirostrum*: 1) the genus *Ceratotriccus* should be merged with *Idioptilon*; 2) the genera *Tacnitriscus* and *Poecilotriccus* should be moved to

positions immediately preceding that of *Todirostrum*, reflecting their affinities with *Todirostrum capitale*; 3) *Todirostrum* and *Idioptilon* should continue to stand as separate genera; 4) the genera *Microcochlearius* and *Sneathlaga* are best merged with *Idioptilon*, while *Oncostoma* should continue to be generically recognized. A phylogeny of the Tody-tyrants and a revised classification of the group are proposed (Figure 4 and Table 1, respectively).

INTRODUCTION

Large complexes of closely related, often morphologically similar species are common in the diverse avifauna of South America. A number of recent studies have focused on ecological relationships between sympatric members of potentially competing species complexes (some examples in Cody, 1974). However, the evolutionary history behind modern distributions and ecological interactions is disregarded in many such studies, at the expense of an adequate perspective on the problems examined. The aim of the present study is to reconstruct this evolutionary background for a widely sympatric group of tropical, insectivorous bird species.

The Tyrannid subfamily Euscarthminae (Hellmayr, 1926) contains roughly 65 species, all of which are small and wholly insectivorous. This subfamily forms one of the four major phylogenetic lineages of small Tyrannidac (Smith, 1970), as shown in Figure 1. The core of the subfamily consists of an assemblage of 32 broad-billed species, placed in 10 genera by de Schau-

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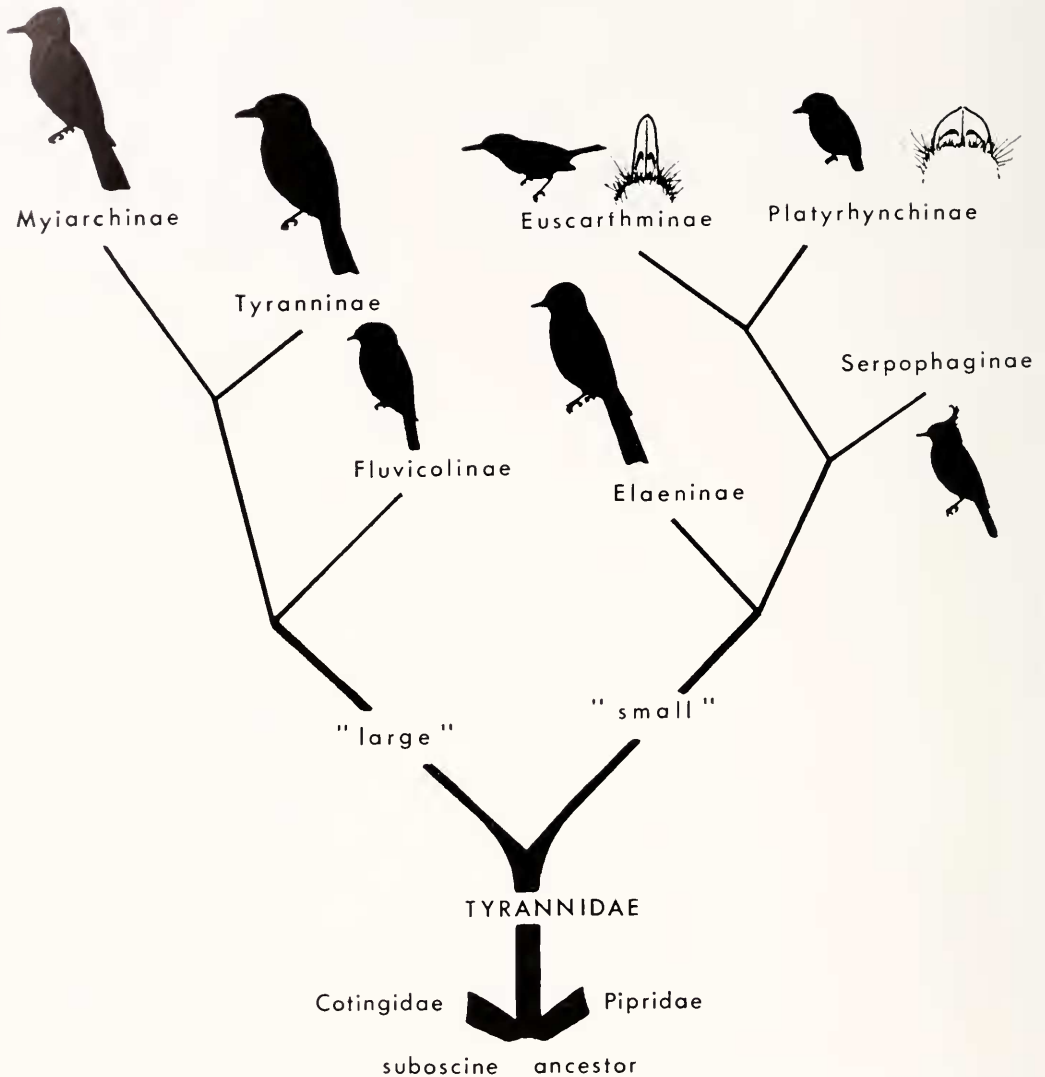


Figure 1. Schematic phylogeny of the family Tyrannidae, showing postulated relationships of the Euscarthminae within the "small" lineage. The seven subfamilies shown are those of Hellmayr (1926). Adapted from W. J. Smith (1970).

see (1966). The genera *Todirostrum* and *Idioptilon* contain 26 of these species (14 and 12 respectively), and each of the remaining 6 species is currently placed in a monotypic genus. Together, the 32 species clearly represent a well-circumscribed, monophyletic group, though their affinities have received little critical attention, and

none at all since Zimmer's brief comments on some of them (1940, 1953, 1955).

As an initial stage in the investigation of the evolution and modern competitive structure of the group, the distributions of all Euscarthmine species were carefully plotted on maps. These distributions were examined in relation to recent theories in

South American biogeography. It became apparent that the patterns of radiation within several subgroups could be traced with reference to Pleistocene climate and vegetation fluctuations, the occurrence of which has been convincingly demonstrated by Haffer (1969, 1974) and Vanzolini and Williams (1970).

Distributional and morphologic data relevant to two particular topics are presented in this paper: 1) A detailed description of speciation patterns in the genus *Todirostrum* is given. The account includes discussion of three related species heretofore placed in the monotypic genera *Poecilotriccus*, *Taeniotriccus*, and *Ceratotriccus*, and four additional species in the genus *Idioptilon*. 2) Certain general implications of the findings to modern biogeographic theory are discussed as they relate to the evolutionary history of certain members of the Euscarthmine assemblage.

Ultimately, the goals of present and forthcoming studies are to determine, 1) the modes of ecological and morphological radiation in this large group of similar, insectivorous species, 2) the varying competitive pressures placed on each other by such closely related forms, and 3) the ways in which various populations selectively respond to these pressures. Such analyses clearly depend upon establishing an evolutionary perspective with which to view modern geographical and ecological conditions. The present study is a first step, therefore, in that it focuses primarily upon the phylogenetic affinities within a subset of the Euscarthminae, and secondarily upon certain ecological implications. A brief discussion of taxonomic considerations germane to this analysis precedes the historical reconstruction of speciation in *Todirostrum*.

TAXONOMIC COMMENTS

Division of distinct morphologic groups into numerous, often monotypic genera was the rule during the early twentieth century classification of the Tyrannidae (e.g., Hellmayr, 1926). With several exceptions this early taxonomy has escaped revision within

the subfamily Euscarthminae. It is now possible to assess the validity of certain of these genera. Specimens of all but two of the 32 Euscarthmine species in the Todytyrant lineage were assembled and examined in conjunction with the present study. The following comments and suggestions are based largely on morphologic patterns and biogeographic considerations covered later.

The species considered in this treatment of the genus *Todirostrum* Lesson, 1831 are those listed by de Schauensee (1966) with the following three exceptions: 1) *T. pictum* is considered to be one of three members of the *chrysocrotaphum* superspecies, as discussed in detail in the speciation section. It should therefore be listed as an allo-species along with *nigriceps* and *chrysocrotaphum*. 2) *T. hypospodium* Berlepsch, 1907 is considered a synonym of *T. sylvia superciliare* Lawrence, 1871. Known from a single unsexed specimen from the Bogotá trade market, *hypospodium* was listed as "a very doubtful species" by de Schauensee (1966: 365). Both Zimmer (1955) and Hellmayr (1926: 308) considered it a dark individual variant of *T. sylvia superciliare*, a fairly common species in the Magdalena Valley near Bogotá. The unlikely event of *hypospodium*'s proven validity as a species would have little bearing on the patterns discussed in this paper. 3) *T. albifacies* Blake, 1959 is considered conspecific with *T. capitale tricolor* (Berla, 1946). Blake (1959) listed the sex of the type (the only specimen collected to date) as uncertain, possibly male. Its close similarity to the female of sexually dimorphic *T. c. capitale* has led Blake and Traylor (personal communication) to reidentify it as a female *tricolor*. The latter form was heretofore known from a single type—unequivocally male—from the Rio Madeira, about 200 km downstream in the same drainage as the type locality of "*albifacies*" (see Fig. 10). Having examined the type of *albifacies* and the photographs in Berla's (1946) description of the male *tricolor*, I

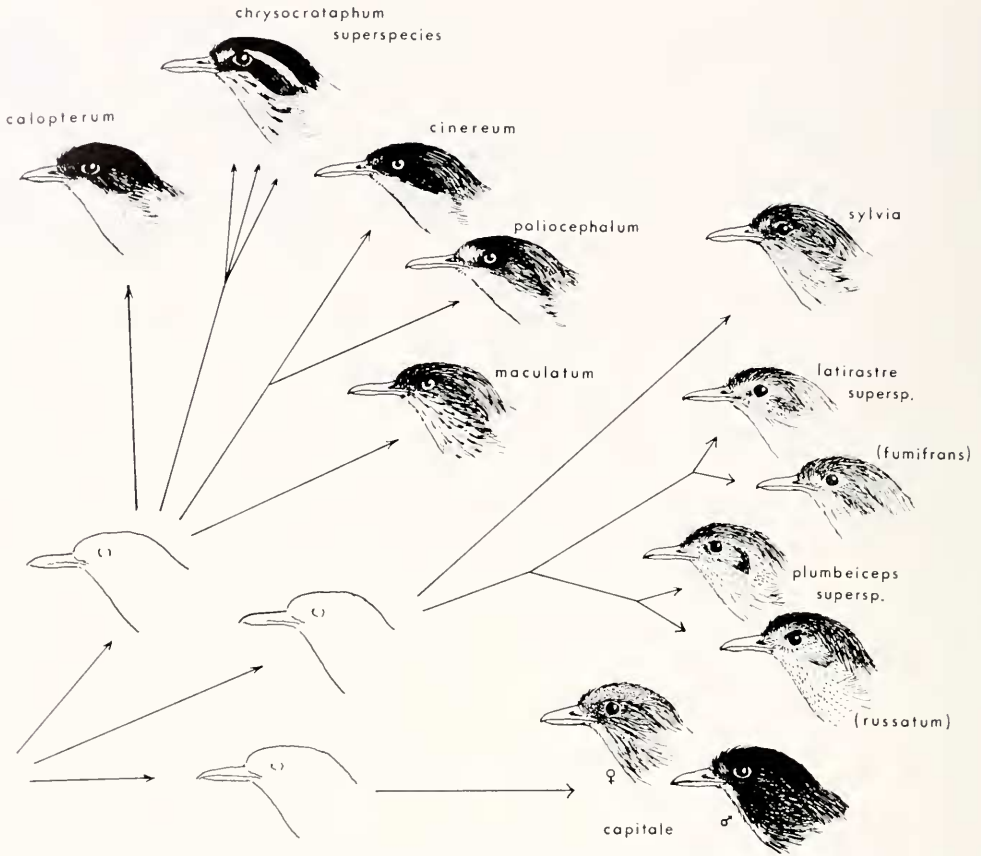


Figure 2. Head patterns in the three species groups making up the genus *Todirostrum*. Eleven of fourteen species are illustrated. Dotted areas about the faces in the *sylvia* group represents buffy plumage; lighter dots represent yellow plumage in the *cinereum* group; the crown of *capitale* female is dark rufous.

consider their similarities to nominate *capitale* sufficient to agree with Zimmer (1955) in treating the two populations as subspecies.

The 14 species in *Todirostrum* fall into three distinct species groups on the basis of bill characteristics and plumage patterns (Fig. 2). The *cinereum* group consists of four distinct species—*calopterum*, *cinereum*, *poliocephalum*, and *maculatum*—and an assemblage of three populations comprising the *chrysocrotaphum* super-species: *chrysocrotaphum*, *nigriceps*, and *pictum*. Each of these seven forms has bright yellow underparts and a dark grey or solid black crown. Back color varies

from rich green (in *chrysocrotaphum*, *maculatum*, and nominate *calopterum*) to grey or grey-green (*cinereum* and *poliocephalum*) to solid black (the isolated Peruvian race of *calopterum*). Throughout its range *maculatum* has numerous thin, brown streaks superimposed on its yellow breast and belly. Thick, solid black streaks form whole or partial necklaces in two members of the *chrysocrotaphum* super-species. All other forms in this species group are clear-breasted. The progenitor for the species group is therefore assumed to have been a clear-breasted form—an assumption that will be used in reconstructing several speciation sequences to follow.

Six species are included here in the *sylvia* species group, though the affinities of *T. senex* remain in doubt. All have grey crowns and light grey underparts, lightening into white or pale yellow on the belly and undertail coverts. Backs of all species are dull green except for that of the southern Venezuelan endemic *russatum*, which has become dark olive-brown. The species group consists of one rather distinct, polytypic species, *T. sylvia*, and five (including *senex*) morphologically similar, allopatric populations here referred to collectively as the "*latirostre* complex." Important plumage differences occur in the amount of buffy or cinnamon coloration in the face and throat, almost entirely lacking in *sylvia* (Fig. 2). The bill of *sylvia* is basally wider than in the *latirostre* complex, and its breast and flanks show more uniform grey than in any of the other species. The extreme similarity between *plumbeiceps* and *russatum* is unequivocal (Zimmer, 1940). I agree with Mayr and Phelps (1967) in considering the latter to be a darkened, Roraiman counterpart of *plumbeiceps*, which is recognized here by placing both within the *plumbeiceps* superspecies. For the present I place *senex* in this group as well, on the basis of its buffy facial and throat plumage (Hellmayr, 1910).

The similarity between patterns of *T. fumifrons* and *T. latirostre*, especially the southeastern populations of the latter, is equivalent to that in the previous superspecies. They are clearly closer to each other than is either species to the *plumbeiceps* superspecies. Particularly considering the parapatry between *latirostre* and *fumifrons* along the Amazon (Fig. 9) it seems appropriate to treat these two as members of a second superspecies (*latirostre*) within the *latirostre* complex.

Todirostrum capitale stands apart from the remaining members of the genus. Its extremely wide bill is shared only by *senex* (Hellmayr, 1926: 309), a species that does not otherwise appear closely related. The

plumage of *capitale* differs from that of all its congeners (partially illustrated in Fig. 2). The male is entirely black above with a white breast and belly, while the female is rich green above with a rufous crown, pearly-grey face and flanks, and white underparts washed with pale yellow under the tail. This pronounced sexual dimorphism is not only unique in the genus, but is quite rare in the entire family Tyrannidae. *T. capitale* stands as an aberrant member of *Todirostrum*, and actually appears to have closer affinities with two species—*Poecilotriccus ruficeps* and *Taeniotriccus andrei*—heretofore placed rather far from it within the Euscarthminae.

The monotypic genus *Poecilotriccus* was originally split from *Todirostrum* on the basis of the bushy rufous crown, relatively shorter bill, and somewhat shortened outer primaries of *ruficeps* (Ridgway, 1907). However, in basic plumage pattern *ruficeps* is remarkably similar to the female of *T. capitale* (see Fig. 3), and *capitale* shows the same short outer remiges. Besides its darkened male plumage, *capitale* differs from *ruficeps* only in its uniquely wide bill and much paler underparts. In general shape the bill of *ruficeps* (Fig. 3) closely approximates those of most other *Todirostrum* species.

Taeniotriccus andrei, a rare species in collections, is divergent from all other Euscarthmine species, especially in its deep, heavy bill. A number of striking similarities it shares with both *capitale* and *ruficeps*, however, provide virtually conclusive evidence for the close relationships among these three species: 1) *T. andrei* is sexually dimorphic; like *capitale*, the males are almost wholly black while females show more olive above (Fig. 3). 2) The bushy, deep rufous crown in both sexes of *andrei*, though interrupted in the center by a black crest, matches exactly the crown color of both *ruficeps* and *capitale* females. 3) Plumage patterns on the underparts of all three species are extremely similar, and resemble no other Euscarthmine species.

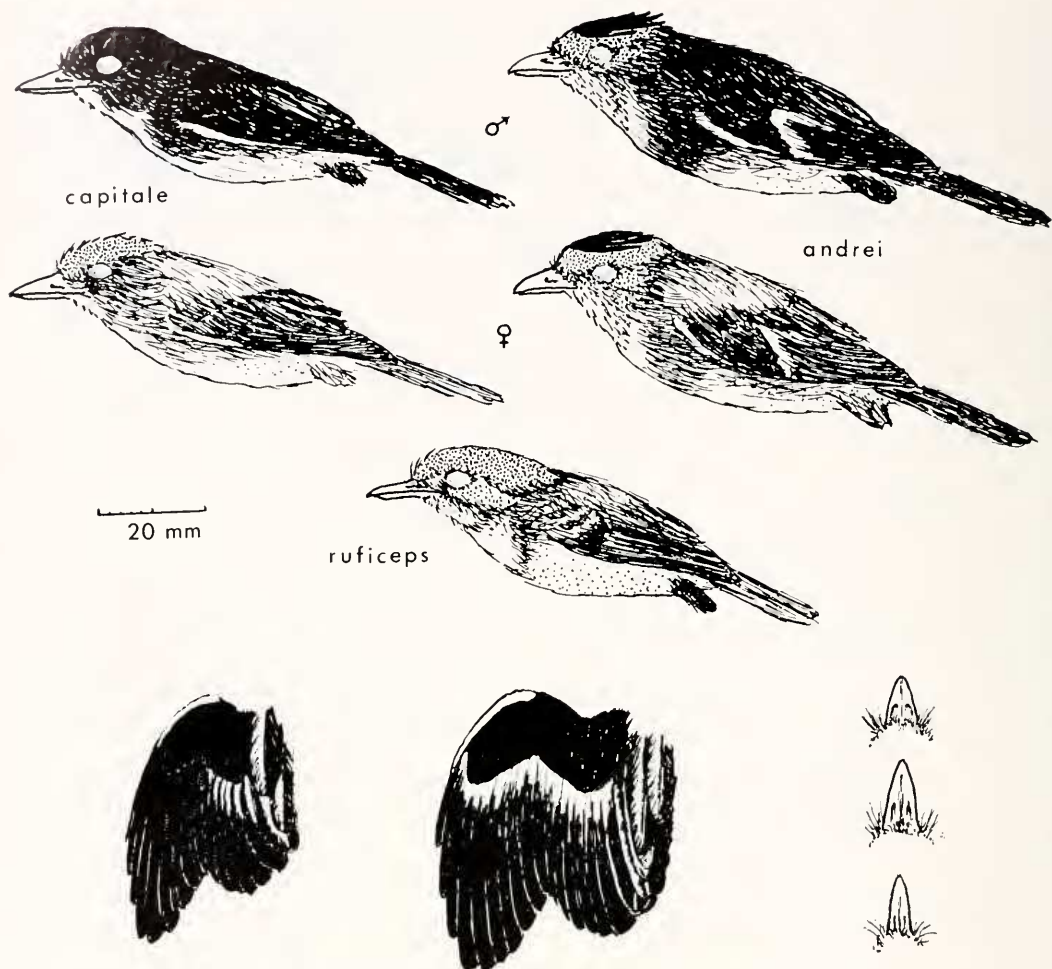


Figure 3. Plumage patterns and bill shapes of species comprising the *Todirotum capitale* lineage. Both *capitale* and *Taeniopteryx andrei* are sexually dimorphic. Crowns of all but male *capitale* are rich rufous (heavy dots). Yellow on the breast (light dots) is most pronounced in *Poecilopteryx ruficeps*, but present in all forms. The hidden white stripe in the wing of *capitale* males (left) further reflects the probable affinities of this species with *andrei* (right). The bill of *ruficeps* (bottom) approaches the typical *Todirotum* shape most closely, while the much heavier bills of *capitale* (middle) and *andrei* (top) have diverged considerably from those of all other Euscarthmine species. This may be associated with their long isolation as relict species within their rapidly diversifying tyrannid lineage.

The throat of *andrei* is light tawny, fading through light grey into a wash of yellow on the belly, but broken by a broad, black pectoral band. This pattern is precisely repeated in *ruficeps*, though the breast band is rather faint and the yellow below quite rich. Furthermore, nominate *capitale* shows a broken black breast band, and the

relict form to the south even retains a complete one (Figure in Berla, 1946). 4) The striking yellow wing stripe in *andrei* appears at the outset to be unique, but even this character is present, if reduced, in *capitale*: the outer webbing of *capitale* specimens' innermost remiges are broadly edged with yellow. When the full wing

is opened, however, yellow bases on additional remiges are revealed, appearing even in the second and third secondaries in some specimens. This hidden yellow band corresponds exactly with the conspicuous wing pattern of *andrei* (see Fig. 3). 5) All three species have black thighs, which are absent in all remaining Euscarthmine species. All also have pale tarsi, though this character is not unique to these three forms. 6) In addition to these morphologic comparisons, biogeographic peculiarities indicate that all three species are secondarily restricted in their distributions (Fig. 10). In sum, the evidence strongly indicates that these species represent relicts from a single, ancestral divergence from a *Todirostrum* precursor.

Affinities among the three species are closer than those between the lineage as a whole and *Todirostrum* or *Idioptilon*. For this reason the current taxonomic positions of the three species are open to question. Possibly, they should be placed together in a separate genus from *Todirostrum*. While it seems the likely course at present, additional behavioral and anatomical study is required before effecting this rather major taxonomic shift. For the present, therefore, it seems sufficient to place the relict genera *Poecilotriccus* Berlepsch, 1884 and *Taenio-*triccus** Berlepsch and Hartert, 1902 immediately before *Todirostrum* in a linear arrangement of the Tyrannidae, and to begin *Todirostrum* with the primitive species *capitale*.

Species in the genus *Idioptilon* Berlepsch, 1907 separate into two distinct plumage types, referred to here as the "brown" and "green" assemblages. The "brown" species group will be dealt with briefly in the speciation analyses to follow, as it appears to be rather closely related to *Todirostrum*. The five members of this group are "*Ceratotriccus furcatus*," *Idioptilon rufigulare*, *I. mirandae*, *I. kaemferi*, and *I. granadense*. They share conspicuously buffy eye-rings, tawny brown facial and throat plumage (darkened into a black throat in *granadense*), light olive backs, and relatively

long tails. *Ceratotriccus furcatus* is a rare, isolated species, restricted to the coastal highlands of southeastern Brazil. Morphologically similar in most respects to the other "brown" species, *furcatus* was originally placed in its own genus on the basis of the lengthened outer rectrices, which result in a somewhat forked tail. While slightly wider distally than in most *Idioptilon* species, the relatively short bill of *furcatus* shows a close affinity to that genus, despite its original description as "*Todirostrum furcatum*." The clear morphologic similarities it shares with the other four members of the "brown" species group are supplemented by biogeographic considerations; all species, including *furcatus*, are secondarily restricted in their distributions (Fig. 11, discussion in *Idioptilon* section).

Recognizing *furcatus* as one of the representatives in a single lineage, the other members of which are all in the genus *Idioptilon*, it seems appropriate at this time to consider it a member of that genus. I propose, therefore, that *Ceratotriccus* Cabanis, 1874 be merged with *Idioptilon* Berlepsch, 1907, and that the species henceforth be recognized as *Idioptilon furcatum* (Lafresnaye, 1846).

Idioptilon kaemferi is included as a race of *I. mirandae* by de Schauensee (1966), even though both Zimmer (1953) and Eisenmann (in de Schauensee, 1966: 366) consider it specifically distinct. The forms are undoubtedly close relatives (specimens of both species examined), but they occur in very local distributions in eastern Brazil separated from each other by more than 2,000 km. Until further information can be obtained, they should be recognized as distinct, and are treated here as members of the *mirandae* superspecies.

Todirostrum senex (known only from the type specimen, stored in the Vienna Museum) may actually be another in this group of relict species, rather than a member of the *plumbeiceps* superspecies as previously speculated. This is suggested by its very rusty face and throat as well as its

exceeding rarity. Its unique bill, however, is wider than that of any modern *Idioptilon* species, and the hypothesis cannot be further examined until the type can be compared critically with the other representatives of the relict species group.

The hypothesis that the "brown" *Idioptilon* assemblage comprises a primitive lineage is supported by the species' distinct similarities to certain members of the genus *Todirostrum*. In overall plumage pattern, and particularly in bill shape, the "brown" group contains species that are morphologically intermediate between typical ("green") *Idioptilon* species and those in the *Todirostrum latirostre* complex. *T. plumbeiceps* and *T. russatum* were, in fact, originally placed in the genus "*Euscarthmornis*," which was later synonymized with *Idioptilon*. Before the transfer of these species into *Todirostrum* (Zimmer, 1940), Hellmayr (1926: 317) had written that (*Idioptilon*) *rufigulare* was nearest to *Euscarthmornis plumbeiceps*. Furthermore, *Idioptilon mirandae* was originally placed in the genus *Todirostrum* (Sneath, 1925). Hellmayr (1926: 305) compared it most closely with *Todirostrum funifrons*, but noted that it "provides the passage to *Euscarthmornis*."

The *latirostre* complex and the "brown" *Idioptilon* species group may actually reflect a morphologic pattern carried by an ancestral form which was to give rise to the entire *Todirostrum* and *Idioptilon* lineages. Their current similarity would thus have resulted from each conserving certain characters in their common ancestry.

Despite the existence of clearly intermediate forms, the generic separation of *Todirostrum* and *Idioptilon*, questioned by de Schauensee (1970), Short (1975), W. J. Smith (personal communication) and others, should be retained for the present. The separation prevents informative super-species and species group divisions from being buried in nomenclature. Additional information, particularly regarding display behavior and vocalizations of most species,

is necessary before the validity of this division can be more accurately reassessed.

More typical *Idioptilon* species comprise the "green" assemblage, to which subgroup *Microcochlearius josephinae*, *Sneathlaga minor*, and *Oncostoma cinerigulare* are closely related. *Oncostoma*—the Bentbill—represents a rather divergent Central American offshoot from *Idioptilon*, and its generic separation appears to be warranted. Smith (in a letter) concurs on the basis of the unique vocalizations of this form in Panama. The first two monotypic genera, on the other hand, are clear continental representatives of the "green" assemblage. Both were separated early in this century on the basis of minor variations from the basic *Idioptilon* bill structure. *M. josephinae* has an excessively wide bill, and *S. minor* shows peculiarly circular, exposed nostrils in many specimens. In all other characters, however, they precisely match those of the "green" *Idioptilon* species group. Recognizing their phyletic positions within one subgroup of a larger, generically recognized taxon, I prefer to merge *Microcochlearius* Chubb, 1919 and *Sneathlaga* Berlepsch, 1909 with *Idioptilon* Berlepsch, 1907. Affinities of *josephinae* remain in some doubt, but it appears certain that *minor* is closest to *I. spodiops* and *I. zosterops* within this species group, based on similarities between the bill and nostril structures in these three species. Little attention is given here to the biogeography of the "green" assemblage, pending field studies of most species.

In order to summarize the phylogenetic affinities within it, a diagram of the entire Tody-tyrant lineage as commented upon in this paper is shown here as Figure 4. While additional behavioral and anatomical data may modify it slightly, the gross relationships indicated are defensible at this time. Phyletic relationships are considered in this paper primarily as a step toward elucidating some biogeographic implications of Tyrannid distributions. Still, when such a synthesis is possible, it should be

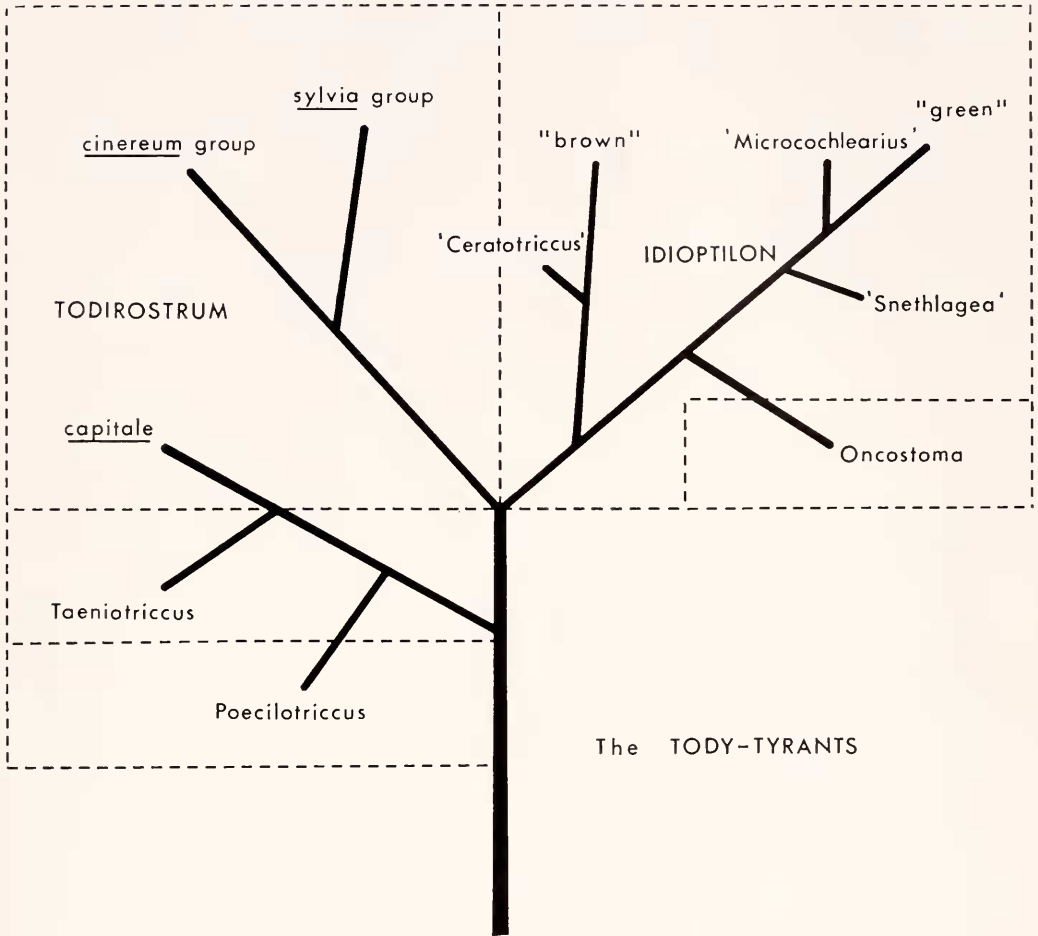


Figure 4. Generic relationships in the Tody-tyrants as commented upon in the text. Dashed lines enclose each lineage whose generic separation warrants continued recognition. Thus "Ceratotriccus," "Microcochlearius" and "Snehlagea" are here grouped into the genus *Idioptilon*. The "brown" species group contains species morphologically intermediate between *Todirostrum* and *Idioptilon*, and is placed within the latter genus on the basis of overall plumage patterns and wing formulae.

incorporated into the basic taxonomy of the group under study. With this in mind, the diagram in Figure 4 includes dotted lines enclosing the generic groups by which, in my view, the Tody-tyrants should now be recognized.

The above suggestions are incorporated into a revision of the broad-billed Euscarthmine tyrannids presented here, along with summaries of the distribution type of each species, as Table 1.

SPECIATION IN *TODIROSTRUM*

Members of the genus *Todirostrum* occur from southern Mexico south throughout tropical and lower subtropical South America to southern Brazil, northern Argentina, and southwestern Bolivia. They are small, secretive birds (16–22 cm, 5–9 gm) generally inhabiting the middle and lower strata of tropical forests and tangled underbrush along forest openings and edges. They forage mostly in thick vege-

TABLE 1. REVISED CLASSIFICATION OF THE TODYTYRANTS (TYRANNIDAE: SUBFAMILY EUSCARTHIMINAE), WITH THE DISTRIBUTION TYPE OF EACH SPECIES INDICATED. SPECIES KNOWN ONLY FROM THEIR TYPE LOCALITY ARE SO MARKED. COLUMNS AND SYMBOLS ARE ADAPTED FROM MAYR AND SHORT (1970) AS FOLLOWS: 1 = LOCALLY DISTRIBUTED, w = WIDESPREAD; COLUMN A = MONOTYPIC SPECIES, COLUMN B = UNCOMPLICATED POLYTYPIC SPECIES (NUMBER OF DESCRIBED RACES INDICATED IN PARENTHESES), COLUMN C = STRONGLY DIFFERENTIATED POLYTYPIC SPECIES (NUMBER OF POPULATIONS IN PARENTHESES), COLUMN D MARKED WITH X IF SPECIES IS A MEMBER OF A SUPERSPECIES. BRACKETS LINK MEMBERS OF SUPERSPECIES.

Species	A	B	C	D
<i>Pocoilatriccus ruficeps</i>		w(4)		
<i>Tacnitiatriccus andrei</i>	w			
<i>Todirostrum</i>				
<i>capitale</i>			1(2)	
<i>cinereum</i> species group				
<i>calopternm</i>			1(2)	
<i>nigriceps</i>	1			X
<i>chrysocrotaphum</i>		w(5)		X
<i>pictum</i>	w			X
<i>cinereum</i> *		w(7)		
<i>poliocephalum</i>	1			
<i>maculatum</i>		w(5)		
<i>sylvia</i> species group				
<i>sylvia</i>			w,1(5)	
<i>latirostre</i>		w(6)		X
<i>fumifrons</i>		1(2)		X
<i>plumbeiceps</i>		w(4)		X
<i>russatum</i>	1			X
<i>senex</i> (type)	1			?
<i>Idioptilon</i>				
"brown" species group				
<i>furcatum</i>	1			
<i>rufignlare</i>	1			
<i>mirandae</i>	1			X
<i>kaemferi</i> (type)	1			X
<i>granadense</i>			w(7)	
"green" species group				
<i>nidipendulumm</i>		w(2)		
<i>striaticolle</i>		w(5)		
<i>spodiops</i>	1			
<i>zosterops</i>			w(4)	
<i>minor</i>		w(2)		
<i>aenigma</i> (type)	1			
<i>inomatum</i> (type)	1			X
<i>margaritaceiventer</i>			w(7)	X
<i>orbitatum</i>	w			
<i>josephinae</i>	1			
<i>Oncostoma cinerignlare</i>			w(2)	

* Includes *T. viridanum*, recently found sympatric with *cinereum* in nw. Venezuela by Phelps.

tation with periodic, rapid flits, picking arthropod prey from the undersides of overhanging leaves. This characteristic foraging method makes use of their peculiarly long, spatulate bills, the most striking morphologic feature of the genus. Habitat preferences of each species are summarized in Table 2.

Reconstruction of the isolation and differentiation of populations, and their patterns of dispersal leading to today's geographic distributions, are based on four assumptions which must be carefully noted at the outset. The first two are closely related, and critical:

1) The primitive *Todirostrum* ancestor, and all descendent forest inhabiting species, were restricted during continental dry periods to small forest "refugia" within their former ranges. This can be inferred from the observation that, with two exceptions discussed presently, modern distributions in this genus occur exclusively within the forested regions of South America. While many populations are currently widespread, most would have been significantly restricted during any period in which the areas of continental humid vegetation were reduced. Substantial evidence now indicates that vast shrinkage of the continental forests during Plio-Pleistocene times did indeed occur (geological, zoological, botanical, and paleobotanical data summarized by Haffer, 1974). It appears safe to suppose, therefore, that the distributions of forest-inhabiting *Todirostrum* precursors were affected by the fragmentation of their favored habitat.

2) Modern populations with local distributions within the continental forests directly reflect their places of origin and differentiation. A number of these local *Todirostrum* populations currently exist, and all of them coincide with refugium sites proposed by Haffer (1974: 145). Actually, a species originating in one area could have been secondarily restricted to another, wholly different region, thus giving the impression of having differentiated

TABLE 2. KNOWN OR DESCRIBED HABITAT PREFERENCES OF SPECIES IN THE GENUS *TODIROSTRUM*. REFERENCE LIST FOR MOST SPECIES IS NOT EXHAUSTIVE, BUT SELECTED TO INCLUDE THE MOST IMPORTANT OR THOROUGH DESCRIPTIONS AVAILABLE. "LOCALITY DATA" REFERS TO DESCRIPTIONS OF COLLECTING LOCALITIES OR NOTES ON SPECIMEN LABELS.

Species	Habitat	References
<i>chrysocrotaphum</i> superspecies	tropical; forest canopy, forest edges, plantations	Skutch (1972), Terborgh and Weske (1969), Haver- schmidt (1968), pers. obs.
<i>calopteryx</i>	upper tropical; forest undergrowth near mountains	locality data, pers. obs.
<i>cinereum</i>	tropical, lower subtropical; scrub, open forest undergrowth; coastal mangroves (Cent. Amer.)	Skutch (1930), Slud (1960), Miller (1963), Terborgh and Weske (1969), pers. obs.
<i>poliocephalum</i>	same as <i>cinereum</i>	Sick (1968)
<i>maculatum</i>	tropical; forested creek edges, marshy river bottoms; coastal mangroves (Guianas)	Haverschmidt (1955), locality data, pers. obs.
<i>sylvia</i>	tropical, lower subtropical; dense thickets, scrub, forest understory	Miller (1947), Gilliard (1959), Slud (1960, 1964), pers. obs.
<i>latirostre</i>	tropical; dense forest under- growth, thick tangles, cane- brakes along rivers	Olivares (1955), Terborgh and Weske (1969, pers. comm.), locality data
<i>fumifrons</i>	tropical; tangled underbrush, open thickets, savana edge	Haverschmidt (1968), Novaes (1970)
<i>plumbeiceps</i>	subtropical; thick brush, forest edge	Wetmore (1926), locality data
<i>russatum</i>	subtropical; atop cerros in Venezuelan tableland	Mayr and Phelps (1967)
<i>capitale</i>	tropical; forest	locality data

there. Since we have no means of proving otherwise, it is assumed here that any secondary restriction of a species' distribution coincided with the area in which it was initially isolated. Potential historical inaccuracies resulting from this assumption are of little consequence to the present study, since only the most recent geographic relationships among species are of concern here.

3) Splitting populations during periods of forest contraction resulted in extinctions of daughter populations in some refuges. As forest "islands" decreased in size the smaller areas became decreasingly capable of supporting the regional fauna, and ex-

inction rates in each refuge increased (MacArthur and Wilson, 1967). Hence, if a species that was initially split into four or five separate populations survived at all, it may have done so in only one or two of the refugia.

4) Foraging modes and habitat preferences of certain forest populations shifted or generalized to include more open habitats during isolation (because of increased competition within the shrinking forest islands), permitting colonization of open scrub regions during the dry periods. This applies particularly to populations of *T. cinereum* and *T. sylvia*, both of which currently inhabit vegetation types that may

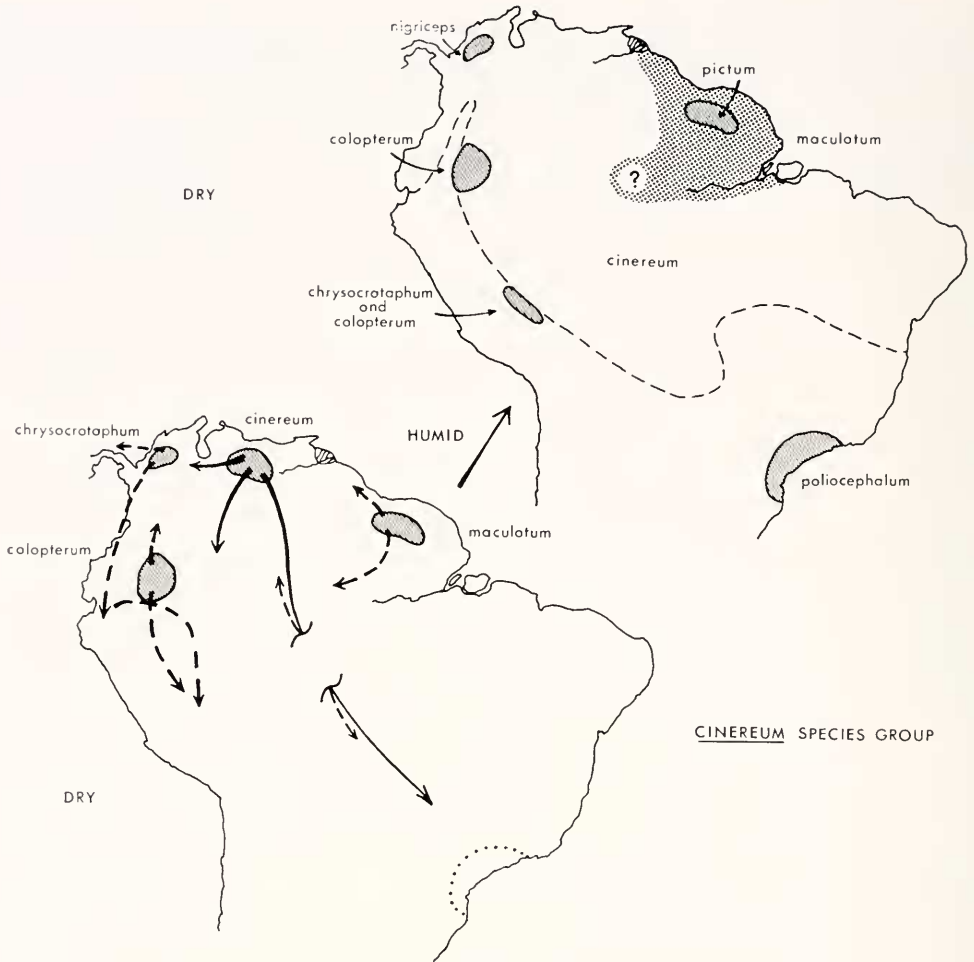


Figure 5a.

Figure 5. Hypothesized patterns of speciation within the *cinereum* (5a) and *sylvia* (5b) species groups in *Todiostrotrum*. Isolation of ancestral populations (shaded areas) during two dry periods and their directions of dispersal from initial refuge sites are diagrammed. During dry periods populations of *cinereum* and *sylvia* dispersed through regions of open vegetation (solid arrows). Dashed lines outline hypothesized distributions of these species during a recent dry period. The distribution of *cinereum* was restricted during a previous humid period, when the central Amazonian forest had returned. This range contraction (see dashed arrows away from Amazonia in 5a) resulted in the isolation of a population in southeastern Brazil, which became *T. poliocephalum*. During humid periods ancestral populations of the modern forest-inhabiting species dispersed (dashed arrows), but contracted again during a recent dry period (upper right diagrams in 5a and 5b). *Todiostrotrum maculatum* might not have been fully restricted to a refugium during the recent dry phase given its current preference for mangroves and streamside vegetation, and the ancestral distribution shown here (heavily dotted region in 5a, with question mark) is speculative.

have been widespread on the continent during the dry phases.

With each climatic cycle, a new magnitude of complexity is naturally added to the distribution patterns in any phyletic group. Hence precise ranges of forms existing prior

to two or three cycles would be impossible to determine from modern distribution data. For this reason, the following reconstruction begins subsequent to the isolation of three species group precursors from the single *Todiostrotrum* ancestor.



Figure 5b.

Figure 5 provides a diagrammatic summary of the speciation patterns derived in detail in the following sections.

Cinereum Species Group

Four populations originally isolated from the precursor of this group have apparently survived, currently represented by five species. *T. poliocephalum* probably originated from a southerly advance of the *T. cinereum* progenitor during a subsequent dry period.

T. calopteryx currently consists of two

divergent races, the nominate (eastern Ecuador and northern Peru) slightly more widespread than *T. c. pulchellum* (southeastern Peru; see Fig. 6). The northern race resembles the other members of this species group, with a green back, black crown, and clear yellow underparts. The Peruvian race, in contrast, has a striking facial pattern with dark malar stripes and deep chestnut loral spots, and its upperparts are entirely black. Assuming that the species originated in one of the two regions to which it is currently restricted (as-



Figure 6. Distribution of three *Todirostrum* species in the *cinereum* species group. The absence of *cinereum* in central Amazonia may be due to the presence there of *T. maculatum* (see text). Diagonal hatching = *cinereum*; dots = *poliocephalum*; squares = two populations of *calopterum* (individual localities).

sumption 2 above), *calopterum* appears to have originated in an eastern Ecuadorian forest refuge (Haffer's large "Napó" refugium). This hypothesis would account for the similarity of the northern race to the other species in the *cinereum* group. The species probably then colonized southward along the post-glacially expanding forests east of the Andes. Its continuous north-south distribution was severed by a return of dry conditions that split the east-Andean forest again into refuges. The southerly population has remained isolated,

and its uniquely divergent plumage attests to a long separation from the northern race.

Distribution and current geographic variation in the *chrysocrotaphum* superspecies are illustrated in Figure 7. The clear yellow underparts of the species group precursor have been retained in *nigriceps* and three races south of the Amazon River. Particularly below its confluence with the Rio Negro, the Amazon is a complete geographic barrier separating streaked from unstreaked populations. Geographic isolation even between the two forms on either

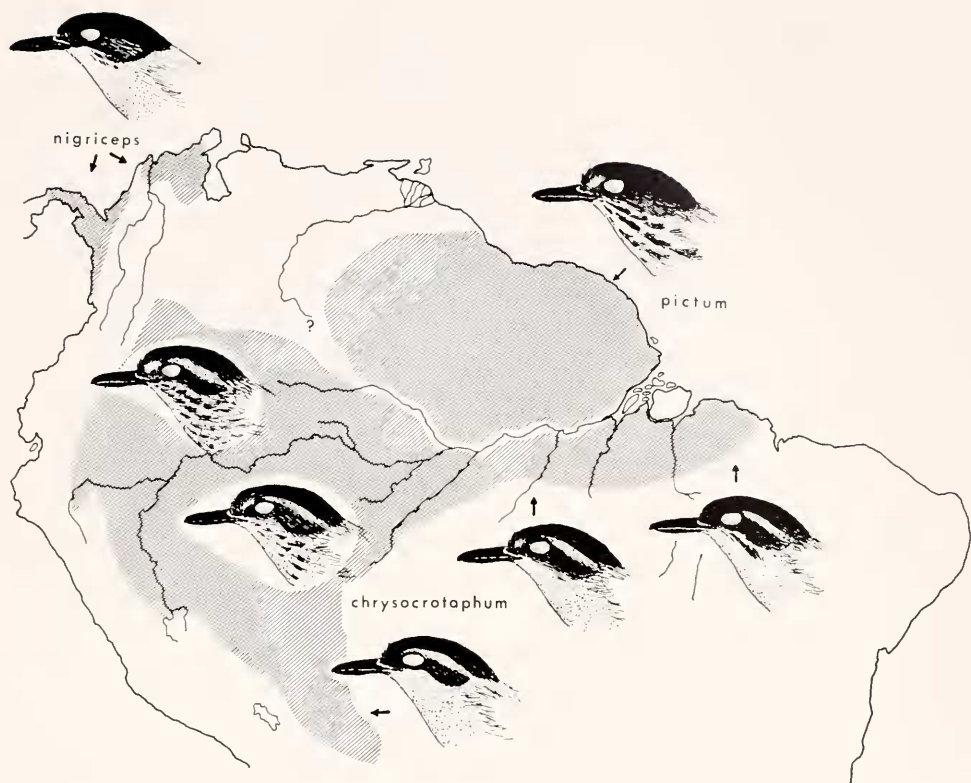


Figure 7. Distribution of the *Todirostrum chrysocrotaphum* superspecies. Representations of the main morphologic types are shown in their approximate geographic positions. From left to right, the five described races of *chrysocrotaphum* are: *guttatum*, *chrysocrotaphum*, *neglectum*, *similis*, and *illigeri*. See text for detailed analysis of this variation.

side of the Rio Negro has been borne out by collections along the lower part of the river. The superspecies thus presents a reliable record of the different forest regions within which its initial populations differentiated.

As previously surmised, the breast streaks of *pictum* and *guttatum* evolved secondarily on the previously clear-breasted form. The original *chrysocrotaphum* stock was therefore isolated either in the southeastern Peruvian forests or in one of the northwestern Colombian forest refuges since these two areas retain clear-breasted populations. During a period of forest expansion the population then spread through the western Amazonian region (where streaks later evolved) to the other region of cur-

rently clear-breasted birds. A Peruvian precursor (of *chrysocrotaphum*) would presumably have had sufficient time before colonizing across the Andes to evolve certain of the patterns it carries today. *T. nigriceps*, however, lacks any trace of the distinct eye stripe of *neglectum*. Furthermore, *nigriceps* retains the white throat characteristic of most other *Todirostrum* species but lost in *neglectum*. Thus it appears that the superspecies precursor differentiated in one of the refuges of northern Colombia (see Fig. 5a), probably during the same period in which the initial *calopteryx* population was isolated in the Napo refuge.

Following initial isolation of the species, the clear-breasted population crossed the

Andes and probably spread through much of its present Amazonian range. The subsequent pattern of differentiation, caused by the return of dry conditions, can be surmised from Figure 7. A distinctive population called *pictum* now ranges from the Guianas west to the Rio Negro. *T. c. neglectum*, with its unstreaked breast, yellow eye stripe, and solid black forecrown, occurs from eastern Bolivia north to the Amazon. The remaining races variously combine characters from both forms. The necklace and loral spot of *pictum* have spread westward, while the eye stripe of *neglectum* has spread north and east. This distribution of characters indicates that forest refuges in the Guianas and in southern Peru were the major centers for Amazonian differentiation during the last major dry period.

As the forest returned, the southern population spread eastward to the Atlantic coast, where it is represented today by the race *illigeri*. The characters of *pictum* have crossed the upper Amazon in western Brazil and Peru, hence certain specimens still assignable to *neglectum* show traces of the necklace and loral spots. Loral spots have now spread eastward again along the southern bank of the Amazon, currently terminating in the race called *similis* west of Rio Tapajoz. *T. c. guttatum*, in eastern Ecuador and northwestern Brazil, shows the full array of characters from both original populations (see Fig. 7). All racial characters in *chrysocrotaphum* shown in the figure are clinal.

The current distribution of characters near the mouth of the Rio Negro and north into southern Venezuela remains somewhat puzzling. The breast and loral markings of *pictum* have moved westward, while the conspicuous eye stripe of *neglectum* remains restricted to the west bank of the Rio Negro and Rio Branco. This is probably due to the sequence by which *pictum* expanded westward, and may indicate a double invasion of the region from the Guianas. The first invasion contributed

breast streaks and loral spots to the west, before open vegetation in middle Amazonia (Haffer, 1967) again separated the eastern and western populations. Upon subsequent dispersal of both populations back toward the Rio Negro, *guttatum* and *pictum* then excluded each other on their respective banks. While a complete series of specimens from northern Brazil may still prove that the forms interbreed there, the available evidence indicates that isolation is complete. *T. pictum* thus represents as clear a geographic representative as *nigriceps* and *chrysocrotaphum* within this interesting superspecies.

Todirostrum cinereum, the most widespread species in the genus, apparently developed its more open habitat preferences during its initial isolation from the species group precursor. The closely related southeast Brazilian endemic, *T. poliocephalum*, occupies similar vegetation types, commonly including garden bushes and shrubbery (Sick, 1968). This latter form differs from *cinereum* only in its more conspicuous yellow lores and distinctly greener back and tail. Their distributions overlap only marginally in southeastern Brazil (see Figure 6) and the southeasterly occurrence of *cinereum* appears to be a reinvasion from the northwest after the population that became *poliocephalum* had been isolated.

The hypothesis that *cinereum* originated in the north (Fig. 5) is supported by two additional lines of evidence. First, the two branches of its range, the races *coloreum* in the south and *cearae* to the north, differ rather sharply in color and measurements, while populations to the west of each differentiate along clines. The indication is that the north and south Brazilian forms colonized independently from a common population northwest of both, and have not shared recent contact with each other. Second, *cinereum* is extremely common in a variety of habitats in northern South America, and occurs in tropical regions throughout Central America as far north as



Figure 8. Distribution of *Todiostrosum maculatum*. Compare its extensive Amazonian distribution with that of *T. cinereum* (Fig. 6), a possible ecological competitor which appears to be excluded from central Amazonia. Diagonal hatching = overall geographic range of *maculatum*. Dots indicate known collecting sites for the species, including one questionable locality.

Vera Cruz, Mexico (Griscom *et al.*, 1957). While fairly common in certain regions of Brazil, it is not nearly as widespread there as might be expected had it originated in the south. The species appears to be better adapted to the more northerly scrub regions, having secondarily advanced south and east into Brazil.

The most recent reappearance of the Amazonian forest probably broke a nearly continuous distribution of *cinereum* in western Amazonia, where it now occurs only along the base of the Andes.

It currently appears that the occurrence of *Todiostrosum maculatum* along river margins in Amazonia contributes to the absence of *cinereum* throughout much of that region (compare Figures 6 and 8). Comparative ecologies of these species are presently being studied to test this hypothesis, but preliminary field data from

Peru and comments by Haverschmidt (1968) already support it. In southeastern Peru (dept. Madre de Dios) *maculatum* inhabits thickly vegetated, early successional margins along rivers, especially bordering beaches, where it forages one to ten meters from the ground (Fitzpatrick, unpublished data). In many respects these habits strongly resemble those of *cinereum* in the Apurimac Valley in central Peru (dept. Ayacucho), where *maculatum* does not occur (Terborgh, personal communication). Furthermore, while *cinereum* is a common mangrove inhabitant in Central and northwestern South America, it is apparently restricted to the drier habitats in Surinam, where *maculatum* has replaced it as the common mangrove Tody-tyrant (Haverschmidt, 1968).

While collecting in the cerrado region of central Brazil has been spotty, that area

does contain a certain fraction of endemic, locally adapted species, including another small Euscarthmine flycatcher (*Euscarthmus rufomarginatus*; Sick, 1965, 1966). It may be that the absence of *cinereum* in central Brazil is also due to the presence there of a better adapted complex of competing species.

The origin and differentiation of *T. maculatum* can be inferred by examining its present clinal variation along the Amazon (distribution shown in Fig. 8). This consists of a gradually lightening crown from the black-crowned race, *amacurensis*, in the Orinoco delta (Eisenmann and Phelps, 1971) to the light grey or green crowns in *signatum* of eastern Peru (Zimmer, 1940: 5-7). There appears also to be a concomitant broadening of the breast streaks toward the west. Both clines leave the Guyana birds much closer to the presumed plumage of the species group precursor (as hypothesized in the taxonomic comments), indicating that *maculatum* originated in a northeastern coastal refuge. Lightening of the crown would have occurred subsequently, as the species spread westward throughout Amazonia. The species is now abundant in mangroves along the Atlantic coast of the Guianas and Venezuela, and occurs along the margins of streams and rivers in the Amazon basin.

Preference for the river margin habitat perhaps explains why, in contrast to the canopy-dwelling *chrysocrotaphum* representatives, *maculatum* does not occur in distinctly isolated geographic forms. During periods of complete separation between true forest populations, such as those in the *chrysocrotaphum* superspecies, the distribution of *maculatum* was probably more continuous along locally moist stream edges, thickets, and canebrakes. Thus *maculatum* populations might have undergone only limited periods of isolation during Pleistocene dry phases, if in fact the species was fragmented at all during that time.

Sylvia Species Group

The distribution of *sylvia* coincides with the scrublands of southern Central America and northern South America (Fig. 9). This species apparently shifted its ecological preferences in a fashion similar to *T. cinereum*, during or immediately following its original isolation. In a subsequent dry period it then spread north into Central America and south along the Atlantic coast. This expanded distribution was interrupted by the return of the modern forests, which restricted nonforest inhabitants as elaborated by Haffer (1967). Two uncommon, relict populations mark the once larger range of *sylvia*: one inhabits the dry, inland savanna region of the Guianas (*T. s. sylvia*) and the other, the caatinga scrub of northeastern Brazil (*T. sylvia schulzi*).

The ecological position of *sylvia* relative to other small Tyrannid species is of considerable interest, though its significance to the species' patterns of distribution and abundance has yet to be worked out. Slud (1964) indicates that *sylvia* generalizes its habitat requirements to include more open shrubbery and second growth forests in regions where *T. cinereum* or *Oncostoma cinerigulare* (a Euscarthmine species closely related to *Todirostrum*) or both are locally absent. This observation, which warrants further field investigation, suggests that *sylvia* is competitively inferior in habitats shared with these relatives. This may explain the rarity or absence of *sylvia* in otherwise suitable habitats throughout northern South America, where *cinereum* is common and widespread. The disappearance of *sylvia* in these areas, initiated by the reduction of its habitat into local islands, may thus have been catalyzed by the presence of a highly successful, congeneric competitor.

T. latirostre is the only wide ranging species in the "*latirostre* complex" and its pattern of variation gives strong evidence for the sequence by which the complex diverged. In eastern Ecuador and north-



Figure 9. Distribution of the six species comprising the *Todirostrum sylvia* species group. All five members of the "latirostre complex" (which excludes *sylvia*) remain allopatric, though *T. senex* is known only from its type locality on the Rio Madeira (Borba). Diagonal hatching downward to left = *plumbeiceps* superspecies (triangles = collecting localities for *russatum*); stippling = *latirostre* superspecies (open circles = collecting localities for *fumifrons*); diagonal hatching downward to right = *sylvia* (X = collecting localities for the two eastern races, *sylvia* and *schulzi*).

eastern Peru, its dark grey crown, cinnamon-buff auricular and ocular regions, light buffy throat, and tawny wingbars all strongly resemble the plumage of *T. plumbeiceps*. Fading of each of these characters south and east of Ecuador results in southeasternmost specimens that closely approach the plumage of *T. fumifrons*. The latter is a rare species inhabiting scrub and

forest-edge habitats east of the range of *latirostre*. The most informative feature of the plumage pattern of *latirostre* is its remarkable resemblance, in the region of the former Napo refuge in eastern Ecuador, to that of the *plumbeiceps* superspecies. This is evidence that the Ecuadorian population of *latirostre* most closely represents the primitive one, and that the species origi-

nated there. This hypothesis is strengthened by the generally northeastern Amazonian distribution of the species today.

Two alternative patterns of speciation in this species group can be hypothesized. First, a recent dry period could have isolated each separate population from a single, wide-ranging species. *T. latirostre* would then have spread eastward into its current range following the return of forests there. This hypothesis, however, fails to account for the particular similarity between *plumbeiceps* and *russatum*, which appear to be immediately descendant from a form already distinct from the *latirostre-fumifrons* ancestor. Furthermore, *plumbeiceps* is currently represented by a Bolivian population which itself has differentiated into recognizable races (Zimmer, 1940). This Bolivian isolation must have occurred during a major dry period which had already isolated *russatum* in Venezuela, since Bolivian specimens of *plumbeiceps* are much closer to those from southeastern Brazil than to the isolated *russatum*.

It appears, instead, that a parent stock for this species group was initially split into a population north of the Andes, which became *sylvia*, and one to the southeast which gave rise to the *latirostre* complex. As open vegetation continued to spread, the cis-Andean form was reduced to isolated populations in the eastern Ecuadorian forests and in southeastern Brazil (see Fig. 5b). This hypothesized sequence is consistent with the observed similarity between *plumbeiceps* and the population of *latirostre* occupying the region of the Napo refuge. As forests returned, the Napo species spread eastward and the Brazilian form spread north and west. As a subsequent dry period began (probably the last major continental arid phase), the southern species had left an isolate on the Venezuelan highlands (now *russatum*) and possibly one in central Brazil (*senex*) before being reduced to its Bolivian-Brazilian range. Further habitat reduction then caused the current gap in the range of *plumbeiceps*

itself (see Fig. 9). The other cis-Andean species, again reduced to its refuge in eastern Ecuador, left an isolate in northeastern Brazil which differentiated into the two races of *T. fumifrons*. Today, *latirostre* has followed the forest and river valleys back eastward into central and southern Amazonia following its last isolation. Its plumage in the drier forested valleys of the Brazilian cerrado appears to be responding to pressures similar to those which affected *fumifrons*. In these areas it has become dull and faded and thus strongly resembles the pattern of its sister species.

The present distribution of *latirostre* reaches, but does not overlap, those of *plumbeiceps* to the south and *fumifrons* to the east. It appears to represent a situation in which close congeners, adapted to their respective place of origin, exclude each other across an intermediate area. Confirmation of this hypothesis requires precise ecological information from different areas within the ranges of each respective species, and at their junctions. These measurements, for most or all species in the group, will be crucial to the completion of the biogeographic analysis initiated here.

Capitale Species Group

Todirostrum capitale clearly originated in the forests of the Napo refuge, to which area it remains almost exclusively restricted (Fig. 10), and appears to represent a deep forest relict of a third population isolated from an original *Todirostrum* ancestor. From the Napo region, its distribution has probably undergone expansions and contractions, but only two specimens have been collected that attest to the species' occurrence elsewhere. The southerly population, *T. capitale tricolor*, originated in a south Peruvian refuge following a southward colonization by the Napo population. It has now extended along the lowland forests of the Rio Madeira drainage into western Brazil, where it apparently remains rare.

Several divergent characteristics of the



Figure 10. Distributions of *Todiostrostrum capitale*, *Taeniotriccus andrei*, and *Poecilotriccus ruficeps*. The latter two genera are monotypic. Morphologic and biogeographic evidence (see text and Figure 3) indicate that these three species comprise a single, relict Tody-tyrant lineage. Vertical hatching = distribution of *Poecilotriccus ruficeps* (small dots = collecting localities); horizontal hatching = distribution of two populations of *Todiostrostrum capitale* (triangles = collecting localities); stippling = distribution of *Taeniotriccus andrei* (open circles = collecting localities).

species, discussed in the taxonomic comments above, suggest that the *capitale* lineage is at least as old as the two major *Todiostrostrum* species groups. Most important, the pronounced sexual dimorphism in *capitale* implies a long period of behavioral as well as morphologic divergence, and attests to the species' long isolation from the other *Todiostrostrum* species. In fact, the *capitale* lineage is probably much older than the two larger species groups, and appears to contain two additional, equally divergent relicts, as shown in the taxonomic section. In addition to their peculiar plumage patterns and bill structures, each of the three species exhibits a secondarily restricted distribution, further indicating the age and relict position of this lineage relative to the other two species groups.

Although *Poecilotriccus ruficeps* is lo-

cally common within its range, its distribution is restricted to a narrow forest zone between 1900 and 2700 m in the Andes from northern Peru to extreme western Venezuela (Fig. 10). Without adequate field data it is impossible to speculate on the precise ecological pressures constraining the distribution of *ruficeps*. However, nearly every Euscarthmine species occupies lowland habitats, and *ruficeps* undoubtedly differentiated originally as a tropical forest species. Narrow altitudinal distributions like that of *ruficeps* may result from invasions into a forest species' original range by one or more species with superior competitive potential. Individuals of the original species that are able to survive and reproduce at higher altitudes eventually provide refuge for the species, gradually forced from its original lowland habitat

through competition. All such shifts are limited by analogous competitive pressures from species already occurring higher on the slopes. Data provided by Terborgh (1971), Terborgh and Weske (1975), and Diamond (1972) give compelling evidence for the action of competition along altitudinal gradients on the distributions of montane birds.

Presumably following range expansions and contractions by *capitale* and *andrei*, both of these species appear to have become rather rare and local. This, too, probably resulted from radiation within closely related Tyrannid species placing increasing competitive pressures on the earlier evolutionary line. As additional successful species were periodically added to the forest fauna, certain species necessarily decreased in abundance. Their overall distributions may thus have been reduced to regions of particularly favorable habitat (possibly the case with *andrei*) or restricted to ever-diminishing zones in which some minimum population level could be maintained (as in *capitale*). These two species thus appear to be engaged in—and possibly losing—an “evolutionary race” as their related competitors continue to radiate. As their populations decline, they either diverge sufficiently in a direction that reduces this competition (causing the peculiarly divergent structures, plumages, and presumably behavior of both *capitale* and *andrei*), or they are ultimately driven to extinction by their competitive environment. A slightly more detailed description of this process is presented in the discussion section.

IDIPTILON AND RELATED SPECIES

As previously discussed, species in *Idioptilon* fall into two plumage types, the “brown” and “green” assemblages, which correspond phyletically with the species groups in *Todirostrum*. The “brown” lineage appears to be phylogenetically intermediate between *Todirostrum* and the typical (“green”) *Idioptilon* lineage. The

interesting and revealing distribution patterns in the relict “brown” species group (Fig. 11) will be discussed briefly here.

Idioptilon rufigulare is a perfect example of an excessively rare montane relict species. It is known from six specimens, all of which were collected between 1200 and 1500 m on isolated Andean ridges in Peru and extreme northern Bolivia. This restricted altitudinal distribution was recently confirmed by J. Terborgh (personal communication) in central Peru, where the species was uncommon but present at 1500 m on a small ridge separated from the main Andes by 100 km of lowland forest. Perhaps once a wide-ranging species, *rufigulare* is now restricted to a narrow, middle altitude zone on certain slopes which, by virtue of their reduced avifauna, are relatively free of lower and higher altitude competitors (Terborgh and Weske, 1975).

Few ecological data are available for the *I. mirandae* superspecies. Clearly, however, the limited ranges of the two members, separated by more than 2000 km, reflect a tiny fraction of their common ancestral distribution in eastern Brazil. Similarly, *furcatum* (formerly “*Ceratotriccus*” *furcatus*) currently occupies an extremely restricted range within the wooded coastal hills of Rio de Janeiro, Brazil.

Of the “brown” *Idioptilon* species, only *granadense* does not appear to have become significantly restricted in its distribution. Morphologically, however, this species is the most divergent in its genus, and, more significant, it is one of only three in the genus that occur at higher elevations. (The other two, *rufigulare* and *spodiops*, are rare mountain relicts.) In isolated north Andean ranges, *granadense* occurs in an altitudinal zone about 1000 m wide (1500 to 2400 m in the Sierra Nevada de Santa Marta, Colombia; 1800 to 2900 m in the Sierra de Perija, Venezuela). On the main Andean slopes, in a more crowded competitive community, its altitudinal limits are more restricted (2280 to 2600 m, west of the Apurimac River, central Peru; Terborgh



Figure 11. Distributions of the five populations in the "brown" *Idioptilon* species group, showing known collecting localities for each species. All but *granadense* are extremely rare, relict species. The upper subtropical altitudinal range of *granadense* (2200–2600 m in central Peru) differs from all other *Idioptilon* species, and appears to be a response to the radiation of assemblages of lowland competitors which has driven the remaining members of this species group close to extinction. Small dots = *granadense*; large dots = *rufifulare*; squares = *mirandae* superspecies (closed = *mirandae*, open = *kaemferi*); triangles = "*Ceratotriccus*" (*Idioptilon*) *furcatus*.

and Weske, 1975). It remains an upper cloud forest inhabitant throughout its range, however, and this habitat is shared by no other close relative.

Distribution and morphologic divergence in the brown *Idioptilon* species group appear analogous to those characterizing the *capitale* lineage in *Todirostrum*. Members of both groups show relict distributions or divergent characters, or both, compared with the other members of their respective genera. As in the *capitale* group, the five brown *Idioptilon* species apparently comprise an early phylogenetic divergence from

the ancestral lineage. Four members have been fragmented or compressed into restricted distributions within the forested tropics and subtropics. The fifth was secondarily forced up into an altitudinal zone that remains unique to the genus. As discussed in the next section, the pressures forcing these early species into their relict conditions apparently resulted from the continued production of new, competitively superior relatives within the tropical forests.

The remaining members of the genus *Idioptilon*, together with the monotypic

genera *Microcochlearius*, *Snethlagea*, and *Oncostoma*, constitute the "green" assemblage. These eleven species appear to form another monophyletic subgroup within the broad-billed Euscarthmine Tyrannids. Additional data on behavior and ecological relationships are required before affinities and distributional patterns in this difficult group can be satisfactorily commented upon. Research is currently underway which may provide some of this information.

DISCUSSION

The *Todirostrum capitale* lineage and the "brown" *Idioptilon* species group are extreme cases illustrating the final stages of a speciation-dispersal-extinction process that appears to be a continental analogue of the "taxon cycle" characterizing island faunas (Wilson, 1961; Ricklefs and Cox, 1972). In this section, some illustrative examples of the main stages in the process precede a brief discussion of the dynamics of this important phenomenon.

In the following outline, nine types of distributional relationships are delimited which summarize the biogeographic "life history" of certain lowland South American bird species. By no means are these categories meant to include all probable intermediate stages in the process to be discussed; rather, only those stages are chosen which characterize members of the Tody-tyrant group dealt with in this paper, and the examples are included under each category.

- 1) Newly isolated populations, presumably still representing a single species.
 - a. races of *Todirostrum sylvia*
 - b. races of *Idioptilon margaritaceiventer* ("green" assemblage)
- 2) Populations apparently isolated prior to the last major dry period; significantly diverged but not yet in secondary contact.
 - a. *Todirostrum nigriceps* — *T. chrysocrotaphum*
 - b. *Todirostrum latirostre* — *T. fumifrons*
 - c. *Todirostrum plumbeiceps* — *T. rusatum*
- 3) Closely related populations currently in contact but not overlapping (parapatric).
 - a. *Todirostrum chrysocrotaphum* — *T. pictum*
 - b. *Todirostrum latirostre* — *T. plumbeiceps*
- 4) Well-differentiated species, partly sympatric but apparently excluding each other geographically over a broad contact zone; presumably similar ecologically.
 - a. *Todirostrum maculatum* — *T. cinereum*
 - b. *Todirostrum cinereum* — *T. poliocephalum*
 - c. *Todirostrum cinereum* — *T. sylvia* (entirely sympatric, but *sylvia*'s range much contracted in presence of *cinereum*; see discussion in speciation section)
- 5) Well-differentiated species, mostly or entirely sympatric; many examples, especially *between* species groups.
 - a. *Todirostrum maculatum* — *T. chrysocrotaphum* superspecies
 - b. *Todirostrum maculatum* — *T. latirostre*
 - c. *Todirostrum plumbeiceps* — *T. poliocephalum*
- 6) Species presumably widespread at one time, now reduced to one or more localized ranges; populations probably declining; often morphologically divergent.
 - a. *Todirostrum capitale*
 - b. *Todirostrum calopteron*
 - c. *Idioptilon furcatum* (formerly *Ceratotropicus*)
 - d. *Idioptilon mirandae* superspecies
- 7) Lowland species still rather widespread, but very rare; either reduced to low absolute density or restricted to rare habitats.

- a. *Taeniotriccus andrei*
 - b. *Microcochlearius josephinae*
- 8) Species with wide altitudinal tolerance, currently forced up to higher altitudes by lowland competitors.
- Example: probably *Todirostrum calopteryx pulchellum*, though conclusive data are lacking; northern race still occurs in lowland forests, but *pulchellum* is rare and restricted to upper tropical zone in southeastern Peru.
- 9) Species related to lowland forms but now restricted to narrow, higher altitudinal zone in the Andes.
- a. *Idioptilon rufigulare* (1200–1500 m)
 - b. *Poecilotriccus ruficeps* (1900–2700 m)
 - c. *Idioptilon granadense* (1800–2900 m, Venezuela; 2200–2600 m, Peru)

Plio-Pleistocene radiation of the suboscines apparently occurred with relatively little competition from other avian groups in South America. Five major suboscine families comprise well over half of the continent's passerine fauna, and the 302 Tyrannid flycatchers, representing one tenth of South America's 2900 land bird species (Smith and Vuilleumier, 1971), radiated into an almost unparalleled array of morphologic groups (summarized by Keast, 1972).

Haffer's extensive work on the zoogeography of lowland South America has given us a clearer picture of how such radiation came about, emphasizing that speciation has been a repetitive process for millions of years. During continental dry periods, presumably associated with world-wide glacial episodes, forest species were split into isolated populations each with the potential for differentiating into a new species. During humid climatic phases, species inhabiting open, nonforest vegetation underwent similar fragmentation. Faunal dispersal within expanding vegetation zones resulted in the splitting of newer species into additional arrays of potentially differentiating

populations during a subsequent climatic cycle.

A geometric increase in species numbers theoretically associated with periodic fragmentations of dispersing populations is naturally damped by ecological factors. Members of each phylogenetic lineage face increasing competitive pressure as the number of closely related species on the continent increases. The probability that regions potentially available for dispersal might already be occupied by related forms increases with the rising number of species in each taxon. In each such lineage, therefore, dispersal of new forms grows increasingly restricted.

Survival of each population hinges upon one of two requisites: 1) it must occupy, either initially or secondarily, an ecological position sufficiently different from those occupied by sympatric species; or, 2) it must maintain a competitive superiority sufficient to cause the decline and eventual extinction of ecologically similar species (e.g., MacArthur, 1972). Radiation within a taxon, and over regional habitats in general, is thus mediated by continual extinctions of new as well as established populations. Extinctions in this context result from competitive interactions in two situations: 1) the regional dispersal of species into areas occupied by competitively inferior species, and 2) island effects within the shrunken areas of the forest refuges (MacArthur and Wilson, 1967).

The dynamic interplay between speciation and extinction has, in short, caused net species compositions within most taxa and over entire geographic areas to move toward equilibrium levels. This process is diagrammatically illustrated in Figure 12.

A number of phenomena variously associated with the process described here are reflected in the current distributions of bird species in lowland South America. Four points will be briefly discussed that appear to be critical to our interpretation of the nine categories of tyrannid distributions presented at the beginning of this section.

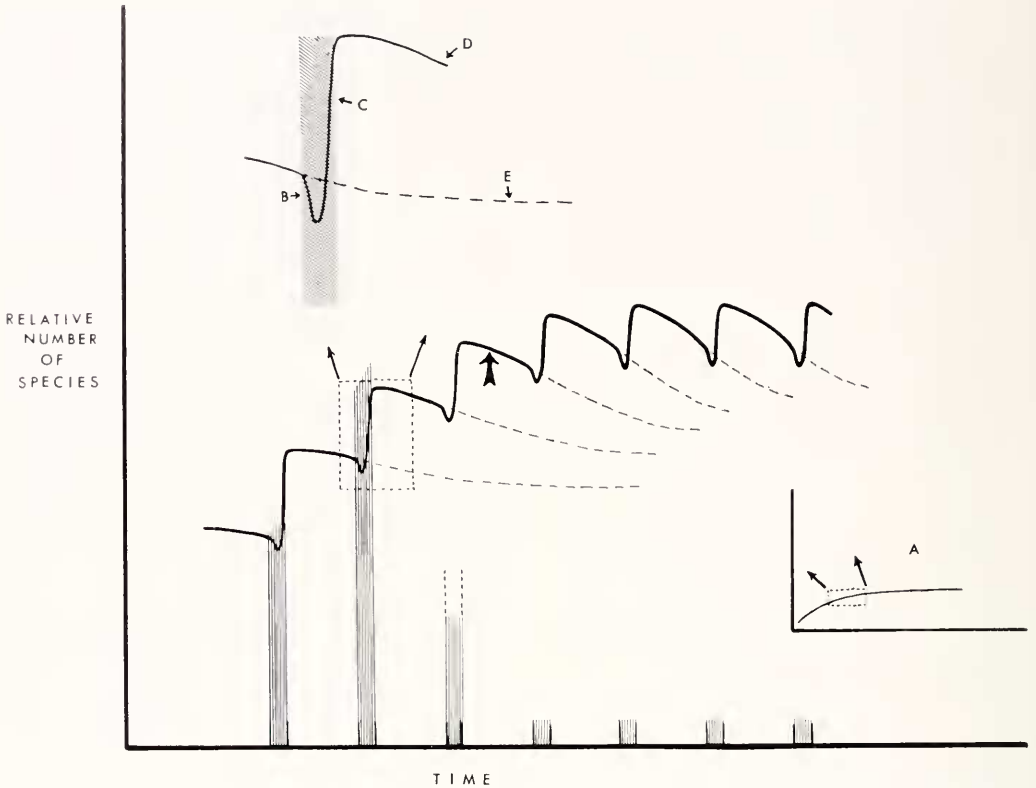


Figure 12. Schematic changes in the relative number of species in the Amazonian forest over time. Shaded areas represent periods of forest fragmentation, associated with dry climatic periods, which split forest species into numerous potentially differentiating populations. New species disperse as the forest returns. These periodic increases in species number are gradually offset by extinctions as competition increases, causing the overall Amazonian diversity to level off at some potential equilibrium value (A). One cycle is shown in detail in the upper left: as the forest contracts, island effects reduce slightly the total number of species (B); differentiation of remaining populations causes an increase in the number of reproductively isolated forms (C); as these disperse with the returning forest, competitive interaction forces species toward extinction, gradually reducing the total number of species (D), which would theoretically smooth out to some stable species composition (E) if the forest remained intact for a long enough period. Note that this stable value increases by smaller increments with each cycle. Heavy arrow indicates hypothesized present position along the species abundance curve.

1) As the number of species increases within a large region like the Amazonian forest the number of forms with small, localized ranges correspondingly increases. Examples of these were used by Haffer (1969) in his reconstruction of forest refuge locations, but few discussions of the ecological implications of such endemics have appeared to date. Endemic species within the Amazonian forest result from the mutually depressing effects on dispersal potential exerted on each other by related species

as each spreads from its respective place of origin. In certain groups of species, each maintains sufficient competitive advantage in its original geographic location to exclude the others from its range. This results in the mosaics of parapatric species illustrated abundantly by Haffer (1974), and by the Tody-tyrants in categories 3 and 4 in the examples presented above.

In other cases, the competitive superiority of a dispersing species over certain others may gradually restrict the distribution of

the latter as the superior species grows increasingly widespread. Ultimately the inferior species will vanish completely, but not before a period of gradually diminishing success within its limited range. Because of the variable and potentially great length of this period, we expect to find at any point in time species representing various stages of this contraction (category 6 above). Alternatively, the same gradual decrease in a species' abundance could occur without a corresponding decrease in its geographic distribution. This type of decline might characterize species occupying peculiar, locally distributed habitats, each patch of which would require separate colonization by the complex of superior competitors. A species' overall population could thus decline toward extinction while still occupying a wide range (category 7).

2) An invaded, declining species can alter its mode of habitat utilization and thus escape the competitive pressure causing its decline. In its extreme, this evolutionary strategy might result in a total habitat shift. These types of ecological shifts are discussed by Hamilton (1962) and MacArthur *et al.* (1966) among others. As discussed in the varied literature regarding "character displacement" (reviewed by Grant, 1972), changes in morphology or behavior or both are normally associated with such ecological shifts (as in category 6, above).

3) A shift in altitudinal tolerance can afford refuge for certain populations otherwise doomed to extinction. This process is discussed with respect to Diamond's data on New Guinea bird distributions by MacArthur (1972: 73). As an invading lowland species becomes increasingly common, successful populations of the diminishing species situated up a mountain slope might begin adapting to microclimatic differences associated with the slightly higher altitude. If the species grows sufficiently more successful at the higher altitudes than its lowland competitor, each will have assumed a geographic refuge within which it cannot be forced toward extinction by the other.

Given their inability to stably coexist within a habitat, the pair would thus exclude each other altitudinally (categories 8 and 9). This process might happen repeatedly along mountain ranges, resulting in the "stacking" of species along altitudinal gradients documented by Terborgh (1971) and Diamond (1972).

4) All changes by which a species shifts away from competitors occur most readily in species with small ranges, where gene flow is sufficiently localized to allow rapid spread of more competitively successful morphological or behavioral adaptations. It therefore becomes increasingly easy for a declining species to diverge into a new ecological role as its range is reduced, resulting in the "evolutionary race" introduced earlier with reference to the relict and divergent *T. capitale* lineage. As a species grows decreasingly capable of competing successfully within the community its range or abundance or both diminish. In species with very small ranges (category 6), genetic pressures normally inhibiting rapid changes might be sufficiently low to permit the spread of adaptations enabling the declining species to coexist with its former competitors. Species that are unable to change fast enough or far enough eventually "lose the race" and decline to extinction.

Because of the recency of the last major climatic shift, numbers and distributions of South American bird species are far from stable at this time (Fig. 12). Certain local regions of open vegetation in Venezuela, for example, presently much reduced from their former area, apparently remain richer in species diversity than might be expected on the basis of their small area. Competition and extinction rates presumably remain high in these areas. Forest regions that remained intact during Pleistocene dry periods appear to be zones in which endemic species, which have survived but are declining, now co-occur with a dispersing, pan-Amazonian fauna. The result is an unstably large number of species

in these zones compared with the avifauna in the surrounding forest. Terborgh (1973) discusses the kinetics of these historical components to local and continental species diversity with respect to plant communities.

Evidence from the Tody-tyrant distributions presented here supports the assertion that avian distributions within Amazonia are not currently in a steady state. Certain populations are probably still dispersing, other local endemics appear doomed to extinction. However, huge time periods are undoubtedly required for dispersing species to force others entirely out of existence. Indeed, the continent is not likely to remain in its present condition long enough for its fauna ever to settle into a stable composition. Rather, a new cycle of isolations and dispersal will again scramble the distributions of its species, and the dynamic processes outlined above will begin on a new array of populations. These geographic processes appear to have been the prime generators of the diverse avian composition inhabiting the South American lowlands.

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